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Review

On the gestural origins of language: what baboons' gestures and brain have told us after 15 years of research

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Nonhuman primates mostly communicate not only with a rich vocal repertoire but also with manual and body gestures. In contrast to great apes, this latter communicative gestural system has been poorly investigated in monkeys. In the last 15 years, the gestural research we conducted in the baboons *Papio anubis*, an Old World monkey species, have shown potential direct evolutionary continuities with some key properties of language such as intentionality, referentiality, learning flexibility as well as its underlying lateralization and hemispheric specialization of the brain. According to these collective findings, which are congruent with the ones reported in great apes, it is thus not excluded that features of gestural communication shared between humans, great apes and baboons, may have played a critical role in the phylogenetic roots of language and dated back, not to the Hominidae evolution, but rather to their much older catarrhine common ancestor 25-40 million years ago.

KEY WORDS: gestural communication, hemispheric specialization, handedness, primates, language evolution.

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Running head: Gestural communication and brain in monkeys

INTRODUCTION

Our research line on gestural communication, just started in the summer 2004 thanks to a baboon display. I observed a social group of baboons *Papio anubis* at the CNRS Primatology Station in South-East of France while I was under the supervision of Prof. Jacques Vauclair (Meguerditchian & Vauclair 2006). A young male walked towards me, then stopped dead. He fixed his gaze on mine and began to repeatedly slam his right hand against the ground (Fig. 1). I remained impassive, but he started again, then changed his strategy: he opened his mouth, raised his eyebrows when widening his eyes, hit the ground again several times with one hand, snapped his teeth, shook his head, suddenly stood up, then fell back on his feet, rubbed forward its both hands on the ground. I took a step forward and here he was running away, before coming back and repeating his display. In fact, as described initially in baboons by Kummer (1968), the young baboon sought to intimidate me with this silent parade of gestures, between play and threat. It turned out that these behaviors seem to meet all the

criteria of what is called "intentional" communication (Leavens 2004). In fact, in absence of the expected response from me, the young baboon seemed to keep trying to reach its communication goal by repeating his hand slapping gesture and even by changing strategy and reformulating with other body gestures, much like a teacher varies his explanations to make himself understood from the audience. In other words, this gestural "persistence", which is a typical property of intentional communication described in the development of language in infants (Bates 1976), might reflect the ability of the baboon to voluntarily produce and control communication signals (i.e. "hand slap gesture") to inform the partner (i.e., "me") of their goal (i.e., "get away").

In the present paper, before reviewing our research on the gestural system of baboons, I will start by reminding the need for a large comparative approach across animal species, and particularly nonhuman primates, on communication and cognition in order to investigate the multiple phylogenetic roots of language. Then I will review the research we conducted in baboons on some cognitive aspects of their communicative gestural system, as well as, in a last part, their manual lateralization and brain hemispheric specialization in comparison with language organization.

THE COMPARATIVE APPROACH ON THE ORIGINS OF LANGUAGE

Searching first for the speech origins

Human language is an extraordinary and unique mean of communication in the animal kingdom involving complex cognitive functions. To investigate the question of its origins, the study of the communication systems of our primate cousins, especially the great apes, has gained unprecedented interest. At the beginning of this quest, the initial scientific debates focused mostly on the origin of speech-specific features (Boë et al. 2019), such as the anatomical modification of the vocal apparatus, the larynx and the vocal tract, the articulatory capacities, the innervation of the tongue, the development of cerebral control for the production of sounds (e.g., Ploog 2002) as well as the "syntactic" capacity to generate a grammar (Chomsky 1966). However, most of these changes having appeared with the emergence of *Homo sapiens* approximately 350,000 years ago, the origin of the language was quite clear: reduced to its verbal and syntactic faculty, language would have emerged as a single holistic feature with the bifurcation of our species (Chomsky 1966; Crow 2002). This turn of the debate thus excluded for a long time the point of view of primatologists on this question, if it was not to confirm that the apes had indeed neither speech (Hayes 1952), nor syntax (Terrace 1979). Since then, recent studies on monkey vocalizations have challenged the idea that monkeys cannot speak due to the anatomical constraints of their vocal tract. It turned out that these constraints, although accurate, are not sufficient to prevent monkeys from producing vocalizations comparable to human vowels (Boë et al. 2017). The inability to speak was therefore to be sought elsewhere, likely in the organization of their cognitive and cerebral systems.

Dislocating the holistic approach on language origins

What if we looked at language other than through its only verbal and syntactic manifestation? In other words, let's see language, not as an indivisible holistic feature

centered on speech and syntax, but rather as a unique combination of many domain-general cognitive properties essential to its functioning; a multimodal linguistic system extending to communicative hand and body gestures as well as facial expressions. Within such a cleverly orchestrated cognitive assembly, which is unique to human species, are certainly included generative and grammatical properties but also other fundamental domain-general cognitive properties such as intentionality, shared attention, learning flexibility, imitation, empathy, theory of mind, categorization, conceptual mental representation, manipulation of shared symbolic conventions, referential properties, as well as their underlying hemispheric specializations of the brain, etc. The list can go on and on (Fitch 2010).

In making such efforts to dislocate the “language” holistic block, it turns out that each of its cognitive components, taken individually one by one, can potentially be shared with animals and be evolutionary inherited from a much older common ancestor than *Homo sapiens*. Seeking for the origins of language is therefore not seeking for the origin of this human “language holistic block” but rather for the origins of each of its many different cognitive components, thus taking its sources from as many different roots in the history of evolution. Without “categorization” faculty for instance, it would be difficult for us to speak given its critical role in the organization of our lexicon. However, this property is not language-specific and is also useful for organizing our perception of the world. It helps us to sort the information that we perceive and put it into categories (tools, food, predators ...) to understand the world, just like most animals such as mice or pigeons (Soto & Wasserman 2014). This property, which is essential for the organization of language, would thus take root directly in more general capacities of perceptual categorization, capacities widely shared in the animal kingdom. In another example, intentional property is characteristic not only of communication in human language, but also of instrumental actions organized to reach a goal (e.g., “I’m going to grab this object”), an behavior which is also widely spread in animals (de Wit & Dickinson 2009). Associative learning is another example of a simple domain-general property essential to language acquisition: it turned out that even bees are able to learn by association (e.g., Menzel 1993). In evolution of animal cognition, it seems that “nothing is lost, everything is recycled” and the origins of language certainly benefit from it.

For a large comparative primates approach including monkeys

The question of the origins of language should thus be reformulated as follows: how these different cognitive properties, which seem to exist in a compartmentalized manner in certain animals, have, over the course of evolution, started to speak to each other, to work together? How did they end up coordinating to become, in the human species, this unique constellation of interconnected properties involved specifically in language? In this framework, the research on the faculties of animals, and of our primate cousins in particular, has thus become central to investigate the evolution of language and its multiple origins. These researches should be thus not restricted to humans, nor great apes, but be extended to a larger comparative approach including monkeys and other animals. For instance, if two cognitive properties involved in language turn out to work together in the chimpanzee cognition for example, it is not excluded that this trait may date back to their common ancestor around 5-9 million years ago. But if this homology extends to an even more evolutionary distant species, such as the baboon, it may have been inherited from their common ancestor 25-40 million years ago, and so on. Within such an approach, I will focus on the research on gestural communicative system in a more distant species, the baboons, and show how this modality seems to start aggregating, just like in great apes, several key cognitive features of language.

COGNITIVE PROPERTIES OF GESTURAL COMMUNICATION

Language and gesture

Language involves tight links with communicative gestures. First, we often gesticulate simultaneously when we speak in signing notably the meaning of our words, such as bringing closer the index and the thumb in saying “small” (McNeill 1992). Regarding the interactions reported between speech and co-speech gestures, it has been suggested that both modalities might share the same integrated communication system (Gentilucci & Dalla Volta 2007). Second, it is well known that intentional communication in infants developed first with the use of communicative gestures before their first spoken words. Deictic gestures specifically, such as pointing, seem to play an active role in the development of linguistic abilities (e.g., Iverson & Goldin-Meadow 2005). These collective findings highlight the importance of gestures in the language system and question their role in language evolution. A growing number of researchers is supporting the “gestural origins” view that gestural communication may be the first phylogenetic precursor of human language (e.g., Hewes 1973; Corballis 2003; Vauclair 2004; Arbib et al. 2008), which rely mostly on investigation of the properties of the gestural communicative system in great apes, particularly chimpanzees primates.

Intentional and referential properties

Interestingly, research in baboons have also reported that, just like in great apes (e.g. Call & Tomasello 2007), production of communicative gestures involves a combination of critical cognitive domain-general properties of language. For instance, some gesture have been reported to be, not only intentional as mentioned above in the introduction, but also simultaneously referential, which consist of indicating intentionally external object from the environment (i.e., out of reach food) to a social partner (here a human experimenter). This behavior requires to orient the attention of the recipient toward this object with imperative visual pointing gestures (Meunier et al. 2013). In an experimental study conducted in 16 adult baboons using such a food begging paradigm, Bourjade et al. (2014) proposed to contrast conditions in which a focal baboon can point to out-of-reach food in front of an experimenter (1) either facing with eyes open the subject (“attentive partner” condition) or (2) closing her eyes or showing her back to the subject (“inattentive partner” conditions). This study showed that, when the human social partner is inattentive, the baboons are able to adjust voluntarily their gestural signals by increasing their production of “noisy” attention-getting gestures (i.e., hand slapping/bagging to the fence) while the visual pointing gestures proportion was higher in the “attentive partner” condition. This ability to take into account the attentional state of the recipient when signaling is typical from intentional and referential communication.

Flexibility

To these two domain-general properties shared with human language, could be also added and combined the remarkable flexibility of the gestural system in baboons. A recent ethological study conducted by Molesti et al. (2020) using continuous focal sampling

observations in 47 baboons over 1 year, have reported that the gestural repertoire could reach about 67 visual, tactile, and audible gestures in this species. After analyzing 2820 focal sessions (60 sessions of 5 min per subject), this study showed that, just as chimpanzees or other great apes (Hobaiter & Byrne 2011; Liebal et al. 2013), size of gesture repertoires varied across individuals and age class (infants, juveniles, subadults and adults) as repertoire size was found to decrease with age. In addition, after counting the number of different gesture types used within the same context and the number of contexts in which one gesture type was used, it turned out that gestures were used flexibly across different contexts indicating means-ends dissociation. Specifically, while 83.6% of the gesture types of the repertoire were used in more than one context, several gesture types (i.e., from 16 to 56 gestures) were systematically recorded for each of the various documented contexts (i.e., affiliative, play, agonistic, submissive, parental care, sexual, grooming and others). This ethological approach also confirms their intentional properties within intraspecific interactions since baboons produced gestures by looking at the recipient, then waited for a response and adjusted their gestural signals to the conspecific's attentional state (i.e., more visual gestures when the recipient was attending and more tactile gestures when the recipient was not).

Although some of these gestures might be innate (see Byrne et al. 2017), Michael Tomasello (e.g., Tomasello et al. 1985) explains such a variability by proposing that most of the gestures in primates would be learned individually through "ontogenetic ritualization" and that only rare gestures could be socially transmitted through a process of imitation. In other words, the majority of gestures seems to be the result of an individual process starting initially from manual actions which would have been gradually ritualized into communicative signals over the course of the social interactions of the developing individual (Tomasello et al. 1985). This process constitutes a first major difference from the process of language acquisition, the vast majority of shared linguistic conventions being rather transmitted by imitation.

Declarative versus imperative gestures

Another major difference is related to the nature of these gestures: these signals in nonhuman primates do not seem to be "declarative" but rather "imperative"; that is to say that their gestures are limited, most often, to express a self-centered request to a conspecific such as "come play with me", "give me this object". In contrast, it seems difficult for them to referentially communicate to external objects or events for the simple shake of sharing their attention with others such as "look at this bird" (Tomasello et al. 1985). According to Tomasello (2006), given declarative communication requires, as for learning by imitation, to take into account the mental states of others (a skill labelled as "theory of mind"), the lack of this communicative skills might be related to the limitation of their "theory of mind", an ability which remains controversial in nonhuman primates. The existence of "imperative" gestures would rather reflect their ability to learn to associate a gestural response with the goal of the request, via the process of "ontogenetic ritualization", but not to attribute mental states to others.

Nevertheless, such a dichotomy of underlying cognitive processes between imperative versus declarative communication has been questioned (Leavens & Racine 2009; Leavens 2021). It is indeed not excluded that both type of signals might be both simply reinforced socially from the partner through the search of social enhancement in both human and apes, which does not require any high-level social cognitive skills (Leavens et al. 2014; Leavens 2021). In addition, we reported a rare and atypical gesture described in only two female baboon mothers, suggesting not only that baboons can flexibly learn new gestures throughout their life but also that some gestures might be also declarative. In fact, we observed the

emergence of a new intentional referential gesture in two female adult baboons (Polka and Fidji), which consists in searching for mutual gaze with her offspring when rolling between her fingers a food in front of her baby's face (see Fig. 2). An atypical behavior which seems to fully meet the criteria of joint attention and declarative communication and that we interpreted as a way to draw the attention of the offspring toward this external object without direct imperative self-centered purpose from the mother. For both females, those behaviors have been observed only in the first 6 months of the infant's age when the baby is not able to feed himself. We also noticed that these behaviors occurred after each birth of a new infant (in four consecutive birth for Polka and in two consecutive birth for Fidji).

Such a combination of domain-general cognitive properties shared between gestural communication in baboons and language in humans suggest a shared phylogenetical heritage and continuity between these two communicatory systems. To further investigate such a hypothesis and exclude any independent evolutionary convergence, it remains critical to determinate whether the underlying lateralized neural structures of both baboons' gesture and human language are also homologue.

HEMISPHERIC SPECIALIZATION AND GESTURE LATERALIZATION

Hemispheric specialization for language

As many cognitive processes, most language functions involve functional hemispheric specialization of the brain, which reflects the better aptitude of one hemisphere over the other for a given function, and/or inter-hemispheric anatomical differences (Josse & Tzourio-Mazoyer 2004). In a large majority of humans, the left hemisphere is dominant for language functions such as phonology, semantics or sentence processing (Vigneau et al. 2006) and the right-hemisphere is dominant for context processing and prosody (Vigneau et al. 2011). Among such a complex asymmetric neural network, some perisylvian regions play a key-role. These regions include Broca's area (Inferior Frontal Gyrus) within the left frontal lobe, as well as the Superior Temporal Sulcus (STS) in the right temporal lobe and the Planum Temporale in the left temporal lobe. Interestingly, some of these regions for language show also striking structural inter-hemispheric asymmetry in size (i.e., surface, volume or depth of a region greater in a hemisphere in comparison to the other). Although their functional implication remains unclear (e.g., Dorsaint-Pierre et al. 2006; Keller et al. 2011; Tzourio-Mazoyer et al. 2018), some of these structural asymmetries were initially considered as anatomical signatures of evolution of the human brain for language and social cognition (e.g., Crow 2002; Leroy et al. 2015).

Handedness is not links with language lateralization

This hemispheric specialization for language was initially considered as associated to handedness. Nearly 90% of humans are right-handed (Annett 1985). From an evolutionary view point, there was a strong debate as to whether such population-level right-handedness is extended to nonhuman primates or is unique and exclusively related to language emergence and brain specialization for language (Bradshaw & Rogers 1993; Crow 2002; Corballis 2003).

This latter view has been challenged by two sets of evidence. First, as many other studies in terrestrial primates such as humans, chimpanzees and gorillas (Meguerditchian et

al. 2013), we reported that baboons showed population-level right-handedness for bimanual coordination task, although in a much lower degree than in humans (Vauclair et al. 2005; Molesti et al. 2016). Interestingly, just like in humans, we also founds that the direction of handedness was correlated with contralateral depth asymmetry within a section of the central sulcus, which seems to correspond to the posterior border of the motor hand area (Margiotoudi et al. 2019). These findings suggest that handedness is not specific to human evolution and not specific to language emergence. Second, it turned out that direction (left or right) of handedness in humans is rather a poor marker of the direction of hemispheric specialization for language, reflecting thus an independent lateralization phenomena (Groen et al. 2013; Mazoyer et al. 2014; Ocklenburg et al. 2014). This hypothesis find support from evidence showing that about 70% of left-handed individuals showed also similar left-hemispheric lateralization for language than right-handed humans (e.g. Knecht et al. 2000).

Lateralization of gestural communication: a better landmark?

Given its independence from language lateralization, handedness for manipulative action might be thus not a relevant model to investigate in nonhuman primates its evolutionary origin. Regarding the strong links reported in the literature between gestural communication and language in humans (see previous section of the paper) as well as the language-like combination of domain-general cognitive properties found in the gestural system of nonhuman primates, manual lateralization for communicative gestures specifically may constitute a better behavioral candidate.

Our research on the lateralization of gestures in baboons provides support to this hypothesis (Meguerditchian & Vauclair 2006). As found in children and in chimpanzees (Meguerditchian et al. 2010, 2013), gestural communication in baboons showed specific pattern of manual lateralization (see Fig. 3). In fact, we found that communicative gestures, such as the “hand slap” (see Fig. 1), elicited not only a more pronounced degree of right-handedness predominance but also independent individual hand preferences in comparison to handedness for non-communicative bimanual manipulation (Meguerditchian & Vauclair 2006, 2009). These findings speak for a greater dominance of the left-hemisphere for communicative gestures which might involve a different lateralized system from the one related to handedness for manipulative functions. It is thus not excluded that lateralization of communicative gestural system in nonhuman primates might share common prerequisites of brain specialization for human language inherited from a common ancestor (Meguerditchian et al. 2011).

Brain structural asymmetry in baboons for language homologs

A key approach to address this latter hypothesis is to investigate in baboons the lateralization of brain structures related to language area’s homologs. Most brain studies conducted in non-human primates have focused on great apes, particularly chimpanzees, and have reported human-like leftward structural asymmetries of a key language region, the planum temporale (Gannon et al. 1998; Hopkins et al. 1998). In addition, it was found in chimpanzees a contralateral association of asymmetries between (1) inter-hemispheric surfaces of the homologs of Broca’s and Wernicke’s areas (Inferior Frontal Gyrus and Planum Temporale, respectively) and (2) the direction of manual preferences (i.e. right- versus left-hand) for communicative gestures (Tagliabattola et al. 2006; Hopkins & Nir 2010; Meguerditchian et al. 2012).

In our cohort of baboons living in social groups, after analyzing 96 anatomical in vivo cerebral images collected non-invasively using magnetic resonance imaging (MRI), we found that a majority of baboons presented a planum temporale's surface larger in the left hemisphere (Marie et al. 2018, see Fig. 4) in a quasi-identical distribution to the one originally found in humans (Geschwind & Levitsky 1968). We recently replicate this finding in a cohort of 35 newborn baboons, indicating that the leftward planum temporale asymmetry is also, just like in prelinguistic infants or in preterm newborn (e.g., Dubois et al. 2010), an early feature of the brain organization across development (Becker et al. 2021b, in press). In addition, according to our on-going studies in those baboons on another sulcus of interest, the superior temporal sulcus (STS), a significant human-like neuroanatomical depth asymmetry in favor of the right hemisphere was found in a specific portion of this sulcus (Meguerditchian et al. 2016), which was initially considered as a human-specific brain lateralization landmark of social cognition (Leroy et al. 2015).

More importantly, in a recent preprint study focusing on an anatomical marker of the Broca area homolog in baboons (i.e., the depth of the ventral portion of the inferior arcuate sulcus in the frontal lobe), we found that communicative gesturing's lateralization – but not handedness for manipulation – is related to contralateral depth hemispheric asymmetry of this marker (Becker et al. 2021a). In other words, baboons communicating with their right hand showed a larger Broca area's marker in the left hemisphere and vice et versa. Interestingly, in contrast to handedness for object manipulation (see Margiotoudi et al. 2019), gestural communication's lateralization is not associated to the central sulcus depth asymmetry, suggesting a potential double dissociation of handedness' types between manipulative action and gestural communication, as hypothesized in our previous manual lateralization studies. This specific lateralized anatomical signature of communicative gesture within the baboons' frontal cortex provides thus strong additional support for a phylogenetical gestural continuities with language-related frontal hemispheric specialization.

CONCLUSION

Our collective research in baboons suggest that combination of cognitive domain-general properties as well as the asymmetric organization of language areas are not specific to human language but extended to far more distant primate species such as the baboon. Interestingly, all those cognitive, behavioral and brain features seems associated with gestural communication in our primate cousins. It is therefore not excluded that some of these prerequisites of language organization may find some phylogenetical roots in gestural communicative system and be inherited, not from *Homo sapiens* 350,000 years ago, but rather from the more distant common ancestor of baboons, chimpanzees and humans, 25 to 40 million years ago.

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Fig. 1. — A young male intimidates a human observer by quickly slapping his right-hand on the ground.



Fig. 2. — An female adult baboon tries to draw the attention of her offspring toward the piece of fruit that she waves between her fingers. This is the first time that such a “joint attention” gestural behavior has been observed in this species. ©Laboratoire de Psychologie Cognitive, CNRS, Univ. Aix-Marseille.

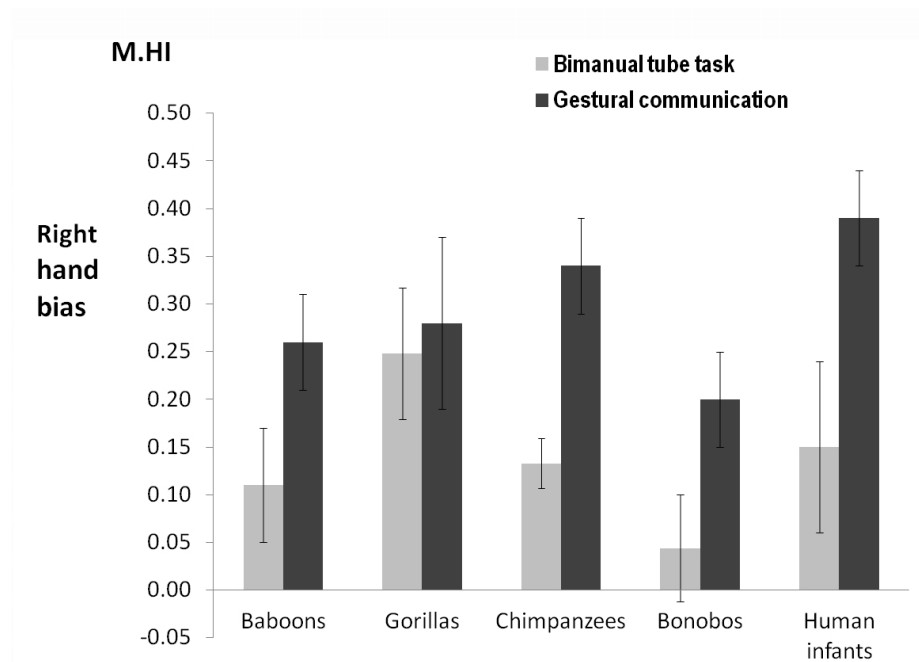


Fig. 3. — Degrees of population-level right-handedness (M.HI: Mean Handedness Index) for species-typical communicative gestures in 162 baboons (Meguerditchian et al. 2011), in 18 gorillas, in 70 chimpanzees (Meguerditchian et al. 2010), in 51 bonobos and whole-hand pointing in 37 human infants (see the review of Meguerditchian et al. 2013). Here, the M.HI are all positive and reflects degree of predominance of right-handedness which are more pronounced for gestural communication in every species – except in gorillas – compared with the bimanual coordinated task. The error bar represents the SE around the M.HI score. Adapted from Meguerditchian et al. (2013).

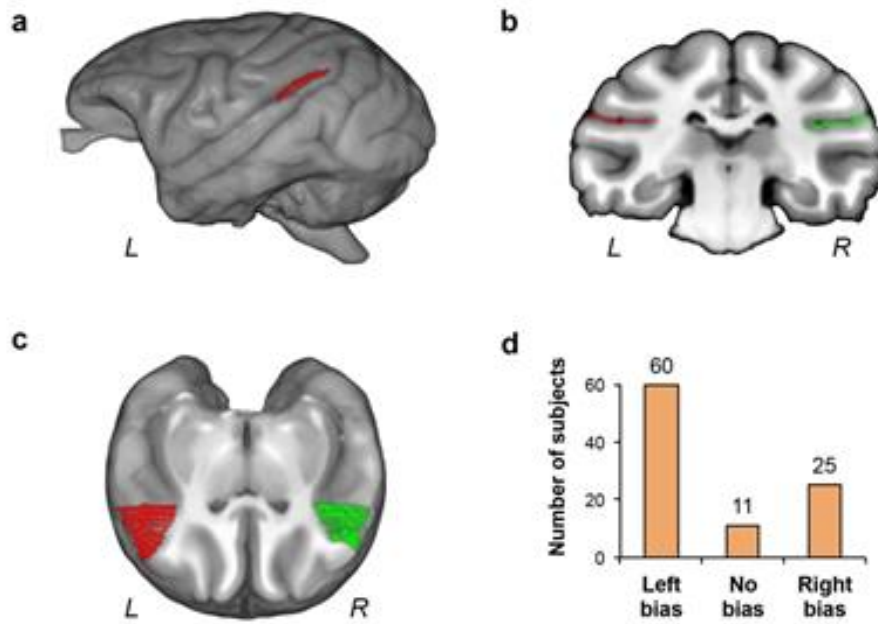


Fig. 4. — Planum temporale's asymmetry quantification in the baboon brain. (a) 3D render of a baboon brain and its delineation of the left planum temporale surface area (red). (b) Overview of the coronal section per coronal section tracing method, one individual coronal section with overlay of left (red) and right planum tracing (green). (c) Oblique section oriented along both planum temporale of a baboon brain (left planum in red, right planum in green) with a clear leftward asymmetry of surface area. (d) Number of left-biased, non-biased and right-biased baboons for the planum temporale surface area according to classification of individual asymmetry quotients (AQ). Adapted from Marie et al. (2018).